PROC. BIOL. SOC. WASH.
93(1), 1980, pp. 50–60

DISTRIBUTION AND SYSTEMATIC RELATIONSHIP OF TWO KINDS OF SHORT-TAILED SHREWS (SORICIDAE: *BLARINA*) IN SOUTH-CENTRAL VIRGINIA

Cathy M. Tate, John F. Pagels, and Charles O. Handley, Jr.

Abstract.—Two kinds of short-tailed shrews that have until recently been regarded as subspecies of a single species, *Blarina brevicauda kirtlandi* and *B. b. carolinensis,* occur in south-central Virginia. Museum collections were examined and additional specimens were collected to delineate further the distribution of these shrews. The two taxa were collected together at two localities. Discriminant function analysis using twelve cranial measurements clearly separated the two kinds in reference samples and in test samples taken in and near areas of sympatry. Only one of 74 test specimens suggested the possibility of intergradition or hybridization. The analysis provided no evidence of panmictic intergradation of the phena in Virginia. This study supports the hypothesis that the two shrews represent distinct species, *B. brevicauda* and *B. carolinensis.*

It has been customary to recognize two species of short-tailed shrews, *Blarina telmalestes* Merriam and *Blarina brevicauda* Say. Four subspecies of the latter are thought to occur in Virginia: *B. b. carolinensis* Bachman, *B. b. churchi* Bole and Moulthrop, *B. b. kirtlandi* Bole and Moulthrop, and *B. b. talpoides* Gapper (Handley and Patton, 1947; Hall and Kelson, 1959). Recently, however, Handley (1971), Genoways and Choate (1972), Jones *et al.* (1975) and Ellis *et al.* (1978) have referred to *B. b. carolinensis* as a separate species, *Blarina carolinensis.*

The geographic distribution of *B. b. kirtlandi* in Virginia was described by Handley and Patton (1947) as the western portion of the state, west of a line drawn from King George County to Prince Edward County not including the high mountains in southwestern Virginia where *B. b. churchi* is found. They showed that *B. carolinensis* occupies the eastern portion of the state except in the Dismal Swamp where it is replaced by *B. telmalestes.* Hall and Kelson (1959) mapped the distribution of *Blarina* in similar fashion, but showed that *B. b. talpoides* occupies the Delmarva Peninsula. Handley (1971) redefined the distribution of *B. brevicauda* and *B. carolinensis* and observed that their ranges overlap in eastern Virginia.

Using characters of skin and skull, Genoways and Choate (1972) studied *B. brevicauda* and *B. carolinensis* in Nebraska. They found that the two

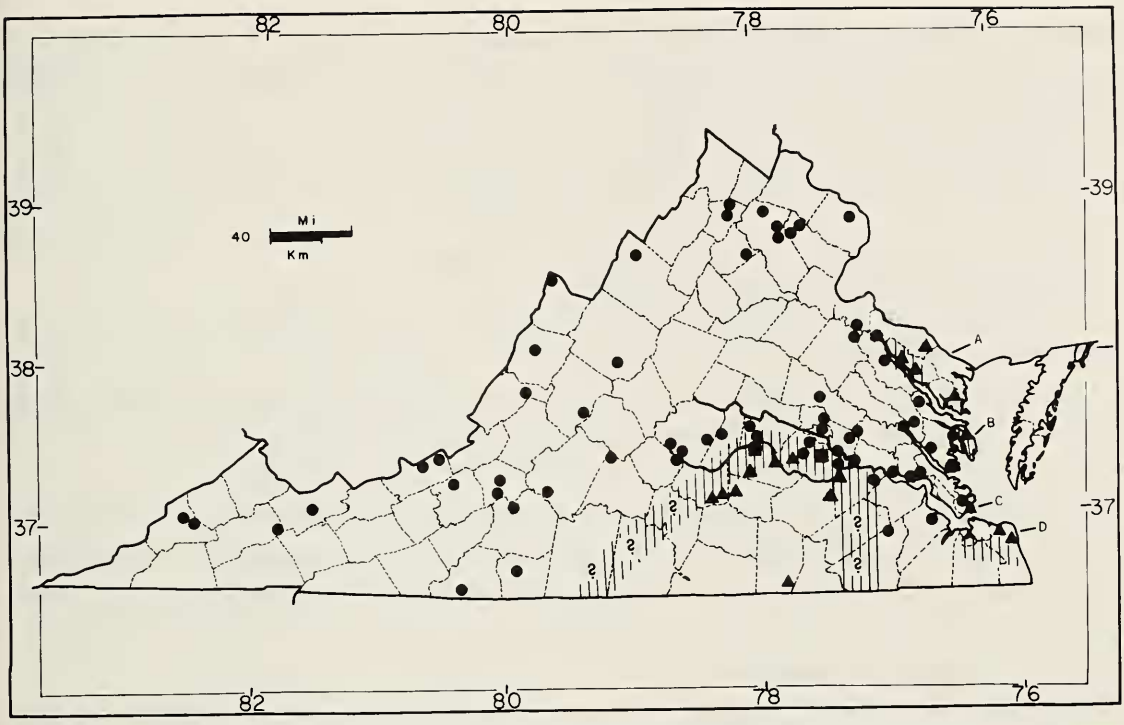

Fig. 1. Distribution of *Blarina brevicauda kirtlandi* (**circles**) and *B. carolinensis* (**triangles**) and areas of sympatry (**squares**) and contiguity (**lined areas**) in Virginia. In areas where collecting localities were close together, the data and triangles may include more than one locality. Dark meandering lines indicate the James and Appomattox Rivers in south-central Virginia. Isolated populations of *B. carolinensis* are indicated at **A**—Northern Neck Peninsula, **B**—Gwynn's Island, **C**—Old Point Comfort, and **D**—Virginia Beach.

taxa did not intergrade there. Ellis *et al.* (1978) found that *B. carolinensis* did not intergrade or hybridize with *B. brevicauda* in Illinois.

Further evidence that *B. brevicauda* and *B. carolinensis* are distinct species is provided by karyotypes (Meylan, 1967; Lee and Zimmerman, 1969; Lund, 1976; Genoways *et al.*, 1977). Genoways *et al.* (1977) found in Nebraska that *B. brevicauda* had a diploid number of 49 or 50 (fundamental number 48) while *B. carolinensis* had a diploid number of 52 (fundamental number 62).

The purpose of the present study was to search for areas of geographic overlap and possible intergradation and hybridization, and to further refine knowledge of the distribution of *B. b. kirtlandi* and *B. carolinensis* in Virginia.

Methods and Materials

For many years Handley accumulated specimens of *Blarina* from Virginia and was fairly well able to define the ranges of *B. brevicauda* and *B. carolinensis* in Tidewater, Virginia (Fig. 1). Later, Tate and Pagels conducted

extensive studies in the lower Piedmont in south-central Virginia where it appeared that the two taxa might be contiguous or sympatric. The resulting collections, housed in the United States National Museum of Natural History (USNM) and the Virginia Commonwealth University Mammal Collection (VCU), together with a few other specimens in the Virginia Polytechnic Institute and State University Museum (VPI), were studied. Emphasis was on the collections of Tate and Pagels.

The field work of Tate and Pagels consisted of sampling along three transects that extended 113 km W, 113 km SW, and 81 km SE from Richmond. These transects contained a total of approximately 210 can (pit) traps that were checked periodically from spring through fall 1976. Museum special traps were used to sample other areas between the transects.

Specimens collected where the two taxa were contiguous or sympatric were compared with reference samples of *B. b. kirtlandi* and *B. carolinensis*. Reference samples were taken from a number of localities over a two state area so that geographic and individual, as well as interspecific, variation could be accounted for.

We aged specimens by toothwear as described by Choate (1968). Young, subadult, adult, and old adult classes were recognized. Only specimens of the subadult and adult age classes were used in test and reference samples. Twelve cranial measurements were taken from each specimen: occipitopremaxillary length, P^4–M^3 length, maxillary breadth, least interorbital breadth, cranial breadth, and zygomatic plate breadth (Choate, 1972); palatal length, postpalatal length, palatal breadth, and nasal width (DeBlase and Martin, 1974); braincase depth (distance from junction of lambdoidal and sagittal crests to the posterior portion of the basioccipital bone anterior to foramen magnum), and skull depth (distance from junction of lambdoidal and sagittal crests to plane intersecting lowest points of skull). Only specimens with complete cranial measurements were used in the discriminant analysis.

Univariate descriptive statistics (mean, standard deviations, minimum values, maximum values, and standard error of the means) were obtained with the MEANS procedure of Statistical Analysis System 76 (Barr *et al.*, 1976). The subprogram DISCRIMINANT of the Statistical Package for Social Sciences (Nie *et al.*, 1970) was used for the discriminant function analysis.

Results and Discussion

Only *B. b. kirtlandi* was taken in the can trap transects west and southeast of the city of Richmond, but both *B. b. kirtlandi* and *B. carolinensis* were captured in the southwestern transect. *Blarina carolinensis* was found in the southern portion of that transect in Prince Edward, Nottoway, and

Amelia counties, and both species were collected in the northern portion of the transect in Chesterfield County. Additional trapping between the western and southeastern transects resulted in the collection of both species at two localities (Fig. 1) and the location of several areas where the ranges of the two species seemed to be contiguous but where no zone of contact could be located.

Sympatry was found on the south bank of the Appomattox River, 9.8 mi N, 0.7 mi E Amelia C. H., Amelia County. At this site a specimen of *B. carolinensis* was collected on 5 November 1976 and two specimens of *B. b. kirtlandi* were taken on 6 November 1976. Sympatry was also found in Chesterfield County (locality 19) where a *B. carolinensis* was captured on 2 November 1976 and a *B. b. kirtlandi* was taken on 9 November 1976. There are two areas in Chesterfield County where the two species were found to be contiguous but no zone of contact could be found. In one area the two taxa were captured 4.7 km apart (*B. carolinensis,* locality 16; *B. b. kirtlandi,* locality 17) and in the southern portion of the county they were taken 14.5 km apart (*B. carolinensis,* City of Colonial Heights; *B. b. kirtlandi,* locality 22).

Standard univariate statistics for twelve cranial measurements and three external measurements of *B. carolinensis* and *B. b. kirtlandi* are given in Table 1. There is only slight overlap in measurements.

Discriminant analysis was conducted using 36 reference specimens of *B. carolinensis* and 70 specimens of *B. b. kirtlandi* (Fig. 2). Standardized discriminant function coefficients (Table 2) show that the cranial breadth was the most heavily weighted, that is, the most discriminating variable, of the measurements taken. Discriminant scores for *B. b. kirtlandi* ranged from −1.379 to 0.013 with a centroid of −0.68537. Discriminant scores for *B. carolinensis* ranged from 0.837 to 1.955 with a centroid of 1.33255.

All test specimens were placed either in the *B. b. kirtlandi* or *B. carolinensis* group with a probability of 1.000 with the exception of three specimens. Test specimens from localities 1 and 31 (Fig. 2) were placed with *B. b. kirtlandi* with 0.999 and 0.987 probability, respectively. The individual from locality 30 was placed into the *B. b. kirtlandi* group with 0.692 probability, indicating a possible hybrid, but is probably best identified as a small *B. b. kirtlandi.*

It should be noted that locality 10 (with two *B. b. kirtlandi*) and locality 11 (with a *B. carolinensis*) actually represent the same place although the locality notations on the specimen labels were different. These specimens, collected in the same habitat (grass-shrub vegetation along a highway right-of-way), showed no evidence of hybridization, intergradation, or convergence in characteristics. In the other area (locality 19) where the two shrews were found to be sympatric, only the larger individual was utilized in the discriminant function analysis because the smaller had a damaged skull. The

Table 1.—Measurements (mm) of *B. b. kirtlandi* and *B. carolinensis* from Virginia and North-central North Carolina.

Character	*B. b. kirtlandi*				*B. carolinensis*			
	Mean	SE	Range	N	Mean	SE	Range	N
Total length	114.33	0.546	98.0–126.0	104	95.59	0.861	84.0–107.0	39
Tail vertebrae	23.75	0.244	13.0–29.0	104	19.33	0.263	15.0–23.0	39
Hind foot	14.42	0.113	8.0–17.0	104	12.28	0.110	11.0–15.0	39
Occipito-premaxillary length	22.03	0.104	20.3–30.0	96	18.79	0.065	17.8–20.0	49
Palatal length	10.04	0.033	9.2–10.7	112	8.45	0.340	7.8–9.0	55
Postpalatal length	9.92	0.034	8.9–10.7	98	8.45	0.360	7.8–9.0	49
P^4–M^3 length	6.06	0.018	5.5–6.5	111	5.24	0.020	4.9–5.5	52
Palatal breadth	6.87	0.021	6.3–7.5	113	6.04	0.023	5.7–6.4	56
Nasal width	2.99	0.013	2.6–3.3	113	2.41	0.013	2.2–2.6	56
Maxillary breadth	7.68	0.029	6.9–8.8	98	6.71	0.030	6.4–7.7	48
Least interorbital breadth	5.67	0.020	5.1–6.3	110	5.06	0.022	4.7–5.5	55
Cranial breadth	12.18	0.113	11.2–12.9	93	10.27	0.043	9.8–10.8	42
Zygomatic plate breadth	2.39	0.014	2.0–2.8	113	2.13	0.016	1.9–2.5	56
Braincase depth	6.36	0.021	5.9–7.0	92	5.48	0.028	5.1–5.9	46
Skull depth	7.18	0.023	6.6–7.7	92	6.25	0.031	5.9–6.7	46

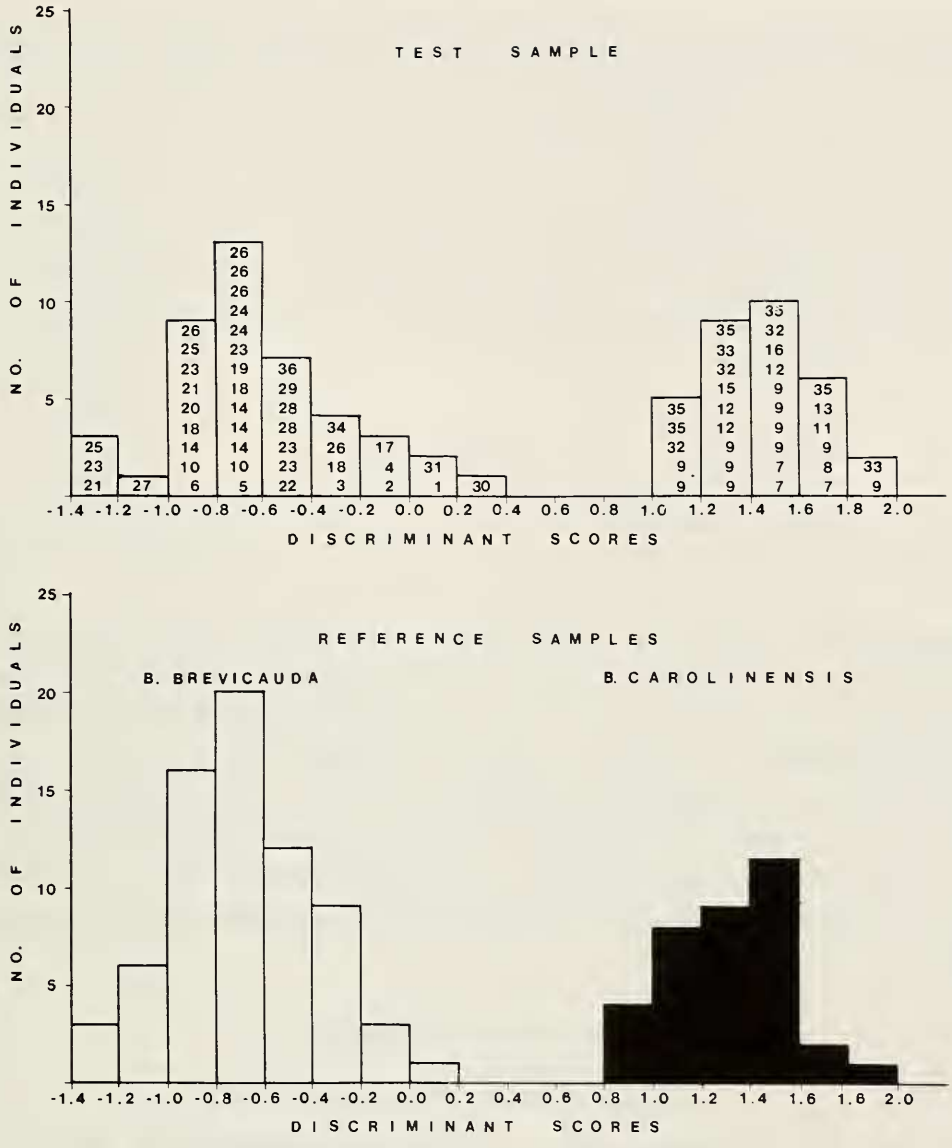

Fig. 2. Frequency histogram of discriminant scores of test and reference samples of *B. brevicauda kirtlandi* and *B. carolinensis* used in this study.

larger shrew was placed into the *B. b. kirtlandi* group by the discriminant analysis but the measurements of the smaller shrew are within the range of *B. carolinensis*. All field identifications agree with the discriminant function classification and, with the possible exception of the specimen from locality 30 discussed above, there was no evidence of intergradation, hybridization, or convergence in characteristics.

Blarina b. kirtlandi and *B. carolinensis* demonstrate a parapatric distribution atypical of Virginia mammals (Fig. 1). The isolated populations of *B. carolinensis* are relicts of a former continuous distribution in eastern Virginia (Handley, 1971). The parapatric distribution found today probably is

Table 2.—Standardized discriminant function coefficient of each discriminating variable.

Discriminating variable	Coefficients
Cranial breadth	−0.33352
Postpalatal length	−0.31472
P^4–M^3 length	−0.23559
Least interorbital breadth	−0.22726
Palatal length	−0.20534
Occipito-premaxillary length	−0.13540
Nasal width	−0.13187
Skull depth	−0.10379
Braincase depth	−0.09565
Palatal breadth	−0.05668
Zygomatic plate breadth	−0.05518
Maxillary breadth	−0.05434

maintained by competition, influenced overall by climatic factors. Graham and Semken (1976) and Handley (1971) suggested that *B. b. kirtlandi* is segregated from *B. carolinensis* by temperature extremes, *B. b. kirtlandi* being adapted to more boreal climates. In areas where the two species are sympatric, no ecological segregation has been recognized. Genoways and Choate (1972) found no ecological separation of *B. b. brevicauda* and *B. carolinensis* in Nebraska, where ". . . all specimens from the zone of contact were trapped in grassy roadside ditches in otherwise highly agricultural areas . . . ."

Specimens Examined

B. carolinensis reference sample

NORTH CAROLINA: Raleigh, USNM (15). VIRGINIA: *Brunswick Co.*: Triplett, Seward Forest, USNM (2). *Dinwiddie Co.*: 6 mi S Petersburg, VCU (1). *Lancaster Co.*: 2 mi NNE Kilmarnock, USNM (15). *Nottoway Co.*: about 1 mi E Burkville, VCU (1). Virginia Beach: Virginia Beach, USNM (2).

B. b. kirtlandi reference sample

VIRGINIA: *Bedford Co.*: Peaks of Otter, USNM (1). *Campbell Co.*: Lynchburg, USNM (4). *Charles City Co.*: 2.4 mi N, 8.7 mi W Charles City Court House (C.H.), VCU (2); E bank Chickahominy River, 5.7 mi S, 10.4 mi E Charles City C.H., VCU (1). *Giles Co.*: Various localities near Mt. Lake, USNM (21). *Gloucester Co.*: near Almonds Wharf, USNM (1); Stubble Farm, near Caphosic, USNM (2). *Hanover Co.*: Ashland, USNM (2). *Henrico Co.*: up to 8 mi E and 5.7 mi N of Richmond, VCU (7). *James City Co.*: Mainland opposite Jamestown, USNM (3); Williamsburg, William and

Mary Biol. Exp. Sta., USNM (5). *King and Queen Co.*: 3 mi SW Mascot, USNM (1). *King William Co.*: 4.5 mi NW West Point, USNM (1). *Middlesex Co.*: Jamaica, USNM (2). *Montgomery Co.*: near Blacksburg, 2,100 ft, USNM (6). *New Kent Co.*: 5 Lakes, 20 mi E Richmond, VCU (1); near Bottom's Bridge, 20 mi E Richmond, VCU (1). *Patrick Co.*: 5 mi SW Stuart, USNM (1). *Prince William Co.*: Catharpin, USNM (1); Buckland, USNM (1). City of Richmond: VCU (3). *Roanoke Co.*: Salem, USNM (1). *Rockbridge Co.*: 2 mi NE Glasgow, USNM (1). *Rockingham Co.*: 1 mi W Broadway, USNM (1).

Test Sample

The letter K preceding the locality number designates *B. b. kirtlandi;* C indicates *B. carolinensis.*

VIRGINIA: *Appomattox Co.*: K-1—Holliday Creek, 4.1 mi N, 10.8 mi E Appomattox C.H., VCU (1). *Buckingham Co.*: K-2—Buckingham-Appomattox State Forest, 5 mi S, 8.5 mi W Buckingham C.H., VCU (1); K-3—Buckingham-Appomattox State Forest, 8.5 mi S, 1.8 mi W Buckingham C.H., VCU (1). *Cumberland Co.*: K-4—4 mi N Cumberland C.H., USNM (1). *Powhatan Co.*: K-5—5 mi WNW Powhatan C.H., USNM (1); K-6—N bank Appomattox River, 3.7 mi S, 2.5 mi W, Powhatan C.H., VCU (1). *Amelia Co.*: C-7—No definite locality, USNM (3); C-8—1.5 mi S, 3.5 mi W Amelia C.H., VCU (1); C-9—Amelia C.H., USNM (10); K-10—S bank Appomattox River, 9.8 mi N, 0.7 mi E of Amelia C.H., VCU (2); C-11—0.6 mi S Appomattox River, 9.5 mi N, 0.3 mi E Amelia C.H., VCU (1); C-12—1.5 mi S of Appomattox River, 8.7 mi N, 0.3 mi E of Amelia C.H., VCU (3); C-13—4.4 mi N, 1 mi E Amelia C.H., VCU (1). *Chesterfield Co.*: K-14—No definite locality, VCU (4); C-15—E bank Appomattox River, 1.5 mi S, 18.75 mi W Chesterfield C.H., VCU (1); C-16—8.3 mi E Appomattox River, 1 mi N, 6.6 mi W Chesterfield C.H., VCU (1); K-17—11.2 mi E Appomattox River, 1.8 mi N, 8.8 mi W Chesterfield C.H., VCU (1); K-18—2.1 mi N, 3.1 mi W Chesterfield C.H., VCU (3); K-19—14 mi SW Richmond, VCU (1); K-20—7 mi N, 0.25 mi W Chesterfield C.H., VCU (1); K-21—5.8 mi N, 0.25 mi E Chesterfield C.H., VCU (2); K-22—Chester, 1.5 mi S, 3.2 mi E Chesterfield C.H., VCU (1); K-23—8.5 mi S Richmond, VCU (5); K-24—3.7 mi W Hopewell, VCU (2); K-25—1.6 mi W Hopewell, VCU (2); K-26—Presquile National Wildlife Refuge, VCU (6). *King George Co.*: K-27—Port Conway, USNM (1). *Prince George Co.*: K-28—16 mi E Hopewell, VCU (2). *Westmoreland Co.*: K-29—Leedstown, USNM (1). *Essex Co.*: K-30—4.6 mi NW Tappahannock, USNM (1). *Richmond Co.*: K-31—1.4 mi SW Newland, USNM (1); C-32—Naylors Bridge, NW Cat Point Creek, USNM (3); C-33—3.6 mi SSW Warsaw, USNM (2). *Isle of Wight Co.*: K-34—Benns Church, USNM (1). *Mathews Co.*: C-35—Gwynn's Island, USNM (1). *Norfolk Co.*: K-36—2 mi N Wallaceton, USNM (1).

Additional Specimens (All Age Classes) Used to Plot the Distribution of *Blarina* in Virginia

B. carolinensis

VIRGINIA: *Amelia Co.*: 3.5 mi S, 6.6 mi W Amelia C.H., VCU (2). *City of Colonial Heights*: City of Colonial Heights, VCU (1). *Dinwiddie Co*: 6 mi SW Petersburg, VCU (1). *Princess Ann Co.* (*Virginia Beach*): Lynnhaven, VPI (5); Kempville, VPI (1). *Prince Edward Co.*: Directly S Prince Edward State Park, VCU (1); 9.5 mi S, 4.8 mi E Prince Edward C.H., VCU (3). *Prince George Co.*. Petersburg (Camp Lee), VPI (4). *Richmond Co.*: 0.5 to 2.2 mi SSE, S, and SW Newland, USNM (6); Warsaw, USNM (1). *Virginia Beach*: Virginia Beach, USNM (2). *Westmoreland Co.*: Kinsale, USNM (1).

B. b. kirtlandi

VIRGINIA: *Alleghany Co.*: Clifton Forge, USNM (6). *Augusta Co.*: 7 mi S Staunton, USNM (2). *Bath Co.*: Clark's Cave, 9 mi SW Williamsville, USNM (12). *Buckingham Co.*: S side Willis River, 3.2 mi S, 7.4 mi E Buckingham C.H., VCU (1); 3.4 mi S, 8.8 mi E Buckingham C.H., VCU (1). *Caroline Co.*: 4 mi SE Port Royal, USNM (2). *Fairfax Co.*: Falls Church, USNM (8). *Fauquier Co.*: 2.5 mi W Thorofare, USNM (2); Rectortown, USNM (1); 6 mi N Warrenton, USNM (6). *Franklin Co.*: 10 mi S Roanoke, VCU (7). *Giles Co.*: Castle Rock, Big. Mt., 4.2 mi NNE Mt. Lake, 4100 ft, USNM (24); Whiterocks Campsite N of Kimbalton, VCU (4); *Gloucester Co.*: 1 mi SSE Bena, USNM (1). *Henry Co.*: 4.5 mi NNW Martinsville, USNM (1). *Highland Co.*: Laurel Fork, 9 mi NNW Monterey, USNM (5); Bear Willow Run, 9.5 mi NNW Monterey, 3200 ft, USNM (2). *Mathews Co.*: Junction Rt. 14 and Rt. 3, USNM (1). *Powhatan Co.*: E side Sallee Creek, 1.7 mi N, 4.5 mi W Powhatan C. H., VCU (2). *Rappahannock Co.*: near Amissville, USNM (1). *Richmond Co.*: 1.4 mi SW Newland, USNM (2). *Roanoke Co.*: Salem, USNM (1); 5 mi S Roanoke, VCU (1). *Russel Co.*: Clinch Mt., Laurel Bed, 6 mi NNW Saltville, 3600 ft, USNM (47). *Southampton Co.*: 2 mi SE Wakefield, USNM (1). *Tazewell Co.*: Burkes Garden, USNM (54). *Warren Co.*: Front Royal, USNM (1); near Cedarville, USNM (3). *Wise Co.*: 5 mi N Wise, USNM (2); 4 mi NE Wise, USNM (1); Hurricane, USNM (3).

Acknowledgments

Results of this study were submitted in partial fulfillment of the requirements for the Master of Science Degree in Biology, Virginia Commonwealth University, by the senior author. Thanks are expressed to Charles R. Blem,

Miles F. Johnson, Richard R. Mills, and Larry Scott, all of Virginia Commonwealth University, for their advice and assistance. Dr. Scott was especially helpful in numerous aspects of the analysis of data. We are grateful to M. D. Marzen, G. C. Scott, and W. H. N. Gutzke, III, for their assistance in field collections. We also express our appreciation to the personnel of the National Fish and Wildlife Laboratory, particularly B. Harvey Bacon, and R. D. Fisher, for numerous forms of assistance, and to the Virginia Polytechnic Institute and State University for the loan of specimens. This research was supported in part by a Visiting Research Student Fellowship at the Smithsonian Institution, and a Grant-in-Aid from the Society of Sigma Xi, both to Tate.

Literature Cited

Barr, A. J., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1976. A users guide to SAS 76.—SAS Institute, Inc., Raleigh. 329 pp.

Choate, J. R. 1968. Dental abnormalities in the short-tailed shrew, *Blarina brevicauda*.—J. Mamm. 49:251–258.

———. 1972. Variation within and among populations of the short-tailed shrew in Connecticut.—J. Mamm. 53:116–128.

DeBlase, A. H., and R. E. Martin. 1974. A manual of mammalogy, with keys to families of the world.—Wm. C. Brown Co., Dubuque. xv + 329 pp.

Ellis, L. S., V. E. Diersing, and D. F. Hoffmeister. 1978. Taxonomic status of short-tailed shrews (*Blarina*) in Illinois.—J. Mamm. 59:305–311.

Genoways, H. H., and J. R. Choate. 1972. A multivariate analysis of systematic relationships among populations of the short-tailed shrews (genus *Blarina*) in Nebraska.—Syst. Zool. 21:106–116.

———, J. C. Patton, III, and J. R. Choate. 1977. Karyotypes of shrews of the genera *Cryptotis* and *Blarina* (Mammalia: Soricidae).—Experientia 33:1294–1295.

Graham, R. W., and H. A. Semkin. 1976. Paleoecological significance of the short-tailed shrew (*Blarina*), with a systematic discussion of *Blarina ozarkensis*.—J. Mamm. 57:433–449.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America.—Ronald Press, New York. 1:xxx + 1–546 + 79.

Handley, C. O., Jr. 1971. Appalachian mammalian geography—Recent Epoch. pp. 263–303 *in* P. C. Holt, R. A. Paterson, and J. P. Hubbard, eds., The distributional history of the biota of the southern Appalachians, Part III.—Res. Div. Monogr. 4, VPI & SU, Blacksburg.

———, and C. P. Patton. 1947. Wild mammals of Virginia.—Virginia Commonwealth Commission of Game and Inland Fisheries, Richmond. 220 pp.

Jones, J. K., Jr., D. C. Carter, and H. H. Genoways. 1975. Revised checklist of North American mammals north of Mexico.—Occas. Papers Mus., Texas Tech Univ. 28:1–14.

Lee, M. R., and E. G. Zimmerman. 1969. Robertsonian polymorphism in the cotton rat, *Sigmodon fulviventer*.—J. Mamm. 50:333–339.

Lund, D. 1976. Chromosome studies of the short-tailed shrew, *Blarina carolinensis*.—Proc. Nebraska Acad. Sci. Affil. Soc., 86th Ann. Meeting:21, abstract.

Meylan, A. 1967. Formules chromosomique et polymorphisme Robertsonian chez *Blarina brevicauda* (Say) (Mammalia: Insectivora).—Canadian J. Zool. 45:1119–1127.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1970. Statistical package for the social sciences.—McGraw-Hill, New York. xxiv + 675 pp.

(CMT and JFP) Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284; (COH) Division of Mammals, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Present address of Tate: Institute of Ecology, University of Georgia, Athens, Georgia 30602.